

## Seed dormancy-breaking and germination requirements of *Drosera anglica*, an insectivorous species of the Northern Hemisphere

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**Abstract** – Seeds of *Drosera anglica* collected in Sweden were dormant at maturity in late summer, and dormancy break occurred during cold stratification. Stratified seeds required light for germination, but light had to be given after temperatures were high enough to be favorable for germination. Seeds stratified in darkness at 5/1 °C and incubated in light at 12/12 h daily temperature regimes of 15/6, 20/10 and 25/15 °C germinated slower and to a significantly lower percentage at each temperature regime than those stratified in light and incubated in light. Length of the stratification period required before seeds would germinate to high percentages depended on (1) whether seeds were in light or in darkness during stratification and during the subsequent incubation period, and (2) the temperature regime during incubation. Seeds collected in 1999 germinated to 4, 24 and 92 % in light at 15/6, 20/10 and 25/15 °C, respectively, after 2 weeks of stratification in light. Seeds stratified in light for 18 weeks and incubated in light at 15/6, 20/10 and 25/15 °C germinated to 87, 95 and 100 %, respectively, while those stratified in darkness for 18 weeks and incubated in light germinated to 6, 82 and 91 %, respectively. Seeds collected from the same site in 1998 and 1999, stratified in light at 5/1 °C and incubated in light at 15/6 °C germinated to 22 and 87 %, respectively, indicating year-to-year variation in degree of dormancy. As dormancy break occurred, the minimum temperature for germination decreased. Thus, seed dormancy is broken in nature by cold stratification during winter, and by spring, seeds are capable of germinating at low habitat temperatures, if they are exposed to light. © 2001 Éditions scientifiques et médicales Elsevier SAS

cold stratification / *Drosera* / insectivorous species / light requirement / seed dormancy / seed germination

### 1. INTRODUCTION

The insectivorous plant genus *Drosera* (commonly called sundews) is cosmopolitan, but many of its about 110 species grow only in the Southern Hemisphere [22], with a concentration of species in Australia [27]. However, at least five species are restricted to the Northern Hemisphere [16], and three of the five are found in Europe: *D. rotundifolia* L., *D. intermedia* Drev. & Hayne and *D. anglica* (Huds.) LePage & W. Bldw. [19]. These three species also occur in North America [16], *D. anglica* and *D. rotundifolia* in Asia [19, 26] and *D. anglica* on mountains in Hawaii [13, 17]. Regardless of the continent on which these three

species occur, they grow in wet boggy sites [13], with *D. anglica* being more tolerant of calcareous soils than the other two species [19].

Recently, there has been considerable interest in germinating seeds of the various taxa of Droseraceae. Newly-germinated seedlings of Droseraceae differ with regard to the amount of cotyledonary tissue that emerges from the seed coats [10], and these morphological characteristics have been used, along with molecular data, to construct cladograms of the family [35]. Conran et al. [10] germinated seeds of about 100 taxa of *Drosera* and recorded number of days from time of sowing until the first seeds germinated and type of seedling morphology. However, from a seed germination ecology perspective these data are not very useful, because dormancy state at time of seed maturation and age of seeds when they were sown are

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not given. Seeds of some taxa may have been non-dormant at maturity, whereas those of others may have been dormant. In species with dormant seeds, dormancy break (afterripening) could have occurred as seeds were stored prior to sowing.

Relatively little information is available on the seed dormancy-breaking and germination requirements of *Drosera*. Seeds of *D. aliciae* Rayn-Hamet from South Africa required a 24-d period of imbibition at 15/10 °C before any germination occurred, but after 34 d ca. 70 % of the seeds had germinated [14]. These authors concluded that dormancy break took place if seeds were subjected to warm, moist conditions but not if they were stored dry. In contrast, seeds of *D. rotundifolia* germinated to 30 % in light at 20/15 °C after 4 months of stratification at 5 °C [18]. Seeds of *D. rotundifolia* mostly germinate in May (spring) in Sweden [29], indicating that dormancy break occurs during winter. Crowder et al. [12] obtained 90–95 % germination of *D. anglica*, *D. intermedia* and *D. rotundifolia* seeds from Saskatchewan, Canada, in light in a glasshouse at 18–22 °C after they had been imbibed in darkness at 10 °C for 8, 16 and 8 weeks, respectively. Seeds of *D. anglica*, *D. intermedia* and *D. rotundifolia*, sown on wet filter paper in plastic Petri dishes kept outdoors in Ontario, Canada, all winter, germinated to 64, 22 and 0 %, respectively, the following spring [12]. Kinzel [21] reported that seeds of *D. anglica*, *D. intermedia* and *D. rotundifolia* required light for germination. Crowder et al. [12] also found that light was required for germination of *D. rotundifolia* and *D. anglica*, but some seeds (percentages not given) of *D. intermedia* germinated in darkness.

The data available from germination studies of *Drosera* spp. restricted to the North Hemisphere raise several questions. (1) How much cold stratification is required to break seed dormancy? (2) As seeds come out of dormancy, what are the temperature requirements for germination? (3) Based on the temperature requirements for germination of non-dormant seeds, when would germination be expected to occur in the habitat? (4) Do stratified seeds require light for germination at some, but not at other, temperatures? (5) If light is given during the stratification period, will seeds subsequently germinate in darkness at simulated spring habitat temperatures? The purpose of our study was to answer these questions using seeds of *D. anglica* collected in Sweden.

The terms non-dormant, conditionally dormant and dormant are used in this paper. Non-dormant seeds germinate over the full range of environmental condi-

tions possible for the species, while dormant seeds do not germinate at any condition [7]. Conditional dormancy (sensu [7, 34]) refers to the series of dormancy states through which seeds progress between dormancy and non-dormancy. When seeds first enter conditional dormancy they germinate over a limited set of environmental conditions, but the range of conditions over which seeds will germinate widens as dormancy break continues. After the seeds gain the ability to germinate over the full range of conditions possible for the taxon or ecotype, they are non-dormant.

## 2. METHODS

### 2.1. Stratification of seeds collected in 1997

Regardless of collection site and year, the alternating temperature regimes used for germination tests of *D. anglica* seeds approximate mean daily maximum and minimum monthly temperatures during the growing season in south-central Sweden, based on 30-year temperature data from Stockholm [25]: May, 14.4 (maximum) and 6.0 (minimum) °C; June, 19.2 and 10.8 °C; July, 21.9 and 14.1 °C; August, 20.2 and 13.3 °C; and September 15.3 and 9.4 °C. Protrusion of the radicle was the criterion for germination, and at the end of all germination tests, ungerminated seeds were pinched with forceps under a dissecting microscope to determine if seeds contained a firm, white thus viable embryo or a soft, gray nonviable one.

Seeds of *D. anglica* were collected on 19 August 1997 in Gästrikland, Sweden (60°55' N), and on 1 September 1997 in Östergötland, Sweden (58°20' N), and dried for 2 and 3 d, respectively, before initiation of experiments. Seeds were placed in 55-mm diameter Petri dishes on two sheets of Munktell 1003 filter paper moistened with de-ionized water; three replications of fifty seeds each were used for each test condition. All dishes were sealed with a strip of parafilm to reduce water loss, and darkness was maintained by wrapping the dishes with two layers of aluminum foil. Seeds from both collections were stratified in darkness at a constant temperature of 1 °C for 12 weeks. After 12 weeks of stratification treatment, seeds from each collection were tested for germination in light (12 h of ca. 40  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , 400–700 nm cool white fluorescent light each day) and in continuous darkness at 12/12 h daily alternating temperature regimes of 15/5, 20/10 and 25/15 °C for 2 weeks. As a control, seeds from each collection were placed in light and in darkness at 15/5, 20/10 and 25/15 °C on the same day the cold stratification treatments were initiated. Control seeds incubated in light were checked for germination at 2-week intervals

for 14 weeks. On the other hand, control seeds incubated in darkness were checked after 2 weeks and discarded, since they had been exposed to light while germination was being checked.

## 2.2. Stratification of seeds collected in 1998 and in 1999

Seeds were sown on Whatman No. 1 filter paper moistened with distilled water in 55-mm Petri dishes; three replications of fifty seeds each were used for each test condition. Tests were conducted in incubators at a 14-h daily photoperiod (ca.  $40 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , 400–700 nm cool white fluorescent light) and in continuous darkness at alternating (12/12 h) temperature regimes of 15/6, 20/10 and 25/15 °C. At each alternating temperature regime, the photoperiod extended from 1 h before to 1 h after the daily high temperature period. All dishes of seeds were wrapped with plastic film to reduce loss of water, and those to be stratified or tested in darkness were wrapped additionally with two layers of aluminum foil.

Seeds of *D. anglica* were collected on 18 September 1998 (same site in Östergötland as in 1997) and dried at room temperatures until 6 October 1998. On this date, seeds were sown on moist filter paper in 36 Petri dishes and placed in light (12 h daily photoperiod,  $40 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) at a 12/12 h daily alternating temperature regimes of 5(day)/1(night) °C for stratification treatments of 2, 6, 12 and 18 weeks in duration. After the various periods of stratification, seeds were transferred from 5/1 to 15/6, 20/10 and 25/15 °C for a 4-week germination test in light. Germination of seeds tested in light was checked after 2 and 4 weeks. Also, on 6 October, nine dishes of seeds were placed in darkness at 5/1 °C. After 18 weeks of stratification, seeds were transferred from 5/1 to 15/6, 20/10 and 25/15 °C for a 4-week germination test in darkness. As a control, fresh seeds were placed in light and in darkness at 15/6, 20/10 and 25/15 °C on 6 October 1998. Control seeds in light were checked at 2-week intervals for 22 weeks, while those in darkness were checked after 4 weeks and discarded, because they had been exposed to light when germination was checked.

Seeds of *D. anglica* were collected on 3 September 1999 (same site in Östergötland as in 1997 and 1998) and dried at room temperatures until 20 September 1999. On this date, seeds were sown on moist filter paper in 72 Petri dishes and placed in light at 5/1 °C for stratification treatments of 2, 4, 6, 8, 10, 12, 14 and 16 weeks in duration. After the various periods of stratification, seeds were transferred from 5/1 to 15/6, 20/10 and 25/15 °C for a 4-week germination test in light. Germination was checked after 2 and 4 weeks. Also, on 20 September, eighteen dishes of seeds were placed in light and 18 in darkness at 5/1 °C. After 18

weeks of stratification, seeds stratified in light and in darkness were tested in both light and in darkness at 15/6, 20/10 and 25/15 °C for 4 weeks. As a control, fresh seeds were placed in light and in darkness at 15/6, 20/10 and 25/15 °C on 20 September 1999. Control seeds in light were checked at 2-week intervals for 22 weeks, while those in darkness were checked after 4 weeks and discarded.

## 2.3. Statistical analyses

A two-way analysis of variance (ANOVA) and comparison of means by protected least significant difference tests (PLSDs,  $P < 0.05$ ) were based on the arcsine-transformed proportion of seeds germinating in each dish after 4 weeks of incubation in light for seeds collected on 18 September 1998 and on 3 September 1999. Also, the same analyses were done on 1999 seeds stratified in darkness and in light for 18 weeks and then incubated in both light and darkness at the three temperature regimes for 4 weeks.

## 2.4. Germination phenology

Seeds of *D. anglica* collected on 18 September 1998 in Östergötland were used in this experiment. Three replications of 200 seeds each were sown, on 22 September 1998, on the surface of commercial peat potting soil in pots (90 mm diameter, 70 mm height) and placed outdoors, 35 km WSW of the collection site. Pots were placed under a table on the north side of a greenhouse, i.e. they were exposed to natural temperature conditions but protected from direct rainfall and direct sunlight. Temperature was recorded approximately every second hour in a parallel pot at 10 mm depth with a TINYTALK-TEMP logger (Orion components Ltd., Chichester, England). The pots were placed in a tray, and the soil was kept constantly moist by adding water to this tray when needed. The pots were inspected for seedlings weekly or biweekly. The experiment was terminated after 14 months.

# 3. RESULTS

## 3.1. Stratification of seeds collected in 1997

None of the fresh (non-stratified) seeds of *D. anglica* from Östergötland germinated after 2 weeks of incubation in either light or darkness, and after 14 weeks in light, one (0.7 %) seed had germinated at 15/5 and one (0.7 %) at 25/15 °C. Seeds given 12 weeks stratification at 1 °C and then incubated in light for 2 weeks germinated to 0, 0 and 13 % at 15/5, 20/10 and 25/15 °C, respectively, while none of the seeds stratified and incubated in darkness germinated. No fresh seeds of *D. anglica* from Gästrikland germinated

**Table I.** Germination percentages (mean  $\pm$  SE) of *Drosera anglica* seeds incubated at three alternating temperature regimes following stratification at 5/1 °C for 0 to 18 weeks<sup>a</sup>. Seeds were collected in 1998. ANOVA and PLSDs were calculated only for germination data after 4 weeks of incubation in light.

Stratification time	Incubation time	Test temperature regimes (°C)		
(week)	(week)	15/6	20/10	25/15
Incubation in light				
0	2	0	0	0
0	4	0 <sup>bC</sup>	0 <sup>aB</sup>	0 <sup>aA</sup>
0	22	0	0	8 ± 2
2	2	0	0	0
2	4	0 <sup>bA</sup>	18 ± 3 <sup>bB</sup>	92 ± 4 <sup>bC</sup>
6	2	0	0	62 ± 6
6	4	0 <sup>bA</sup>	51 ± 12 <sup>cB</sup>	76 ± 4 <sup>cB</sup>
12	2	0	15 ± 4	96 ± 1
12	4	0 <sup>bA</sup>	84 ± 3 <sup>dB</sup>	100 <sup>dC</sup>
18	2	0	0	97 ± 3
18	4	22 ± 3 <sup>aA</sup>	100 <sup>eB</sup>	100 <sup>dB</sup>
Incubation in darkness				
0	4	0	0	0
18	4	0	0	0

<sup>a</sup> Numbers in a column followed by the same lower case letter are not significantly different from each other, and those in a row followed by the same upper case letter are not significantly different from each other.

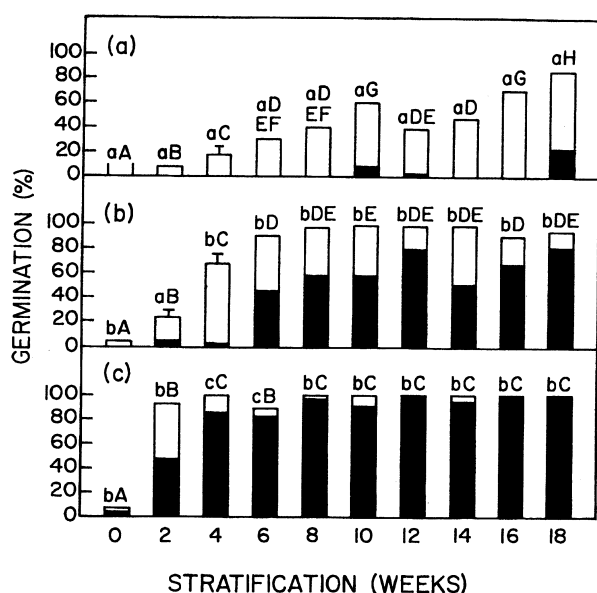
in darkness or in light after 2 and 14 weeks incubation, respectively, and seeds stratified in darkness at 1 °C failed to germinate in light or in darkness at 15/5, 20/10 and 25/15 °C. As verified by data from subsequent studies on seeds from both sites that had been stored dry for 7–13 months in a freezer, 95 and 80 % of the seeds from Gästrikland and Östergötland, respectively, were viable.

### 3.2. Stratification of seeds collected in 1998

Fresh (0 weeks of stratification) seeds of *D. anglica* did not germinate in light or in darkness after 4 weeks of incubation at the three alternating temperature regimes, and after 22 weeks of incubation in light 0, 0 and 8 % of the seeds had germinated at 15/6, 20/10 and 25/15 °C, respectively (table I). Stratification significantly increased germination ( $F_4 = 178.86$ ;  $P < 0.0001$ ). There also was significantly more germination at higher temperatures ( $F_2 = 397.49$ ;  $P < 0.0001$ ), as well as a significant stratification  $\times$  temperature interaction effect ( $F_8 = 36.41$ ;  $P < 0.0001$ ). With an increase in the length of the stratification period (1) germination percentages of seeds incubated in light increased, and (2) the minimum temperature at which seeds would germinate decreased (table I). No seeds germinated in darkness.

### 3.3. Stratification of seeds collected in 1999

Non-stratified seeds of *D. anglica* germinated to 0, 3 and 6 % in light at 15/6, 20/10 and 25/15 °C, respectively, after 4 weeks of incubation (figure 1) and to 2, 7 and 15 %, respectively, after 22 weeks of imbibition. After 4 weeks of incubation, there was no germination of non-stratified seeds in darkness at any temperature regime. Stratification significantly increased germination only in light ( $F_9 = 99.55$ ;  $P < 0.0001$ ). There also was significantly more germination at higher temperatures ( $F_2 = 329.19$ ;  $P < 0.0001$ ), as well as a significant stratification  $\times$  temperature interaction effect ( $F_{18} = 9.18$ ;  $P < 0.0001$ ). As was true for the 1998 seeds, germination percentages of seeds incubated in light increased and the minimum temperature at which seeds would germinate decreased with an increase in length of the stratification period (figure 1). Light was required for germination of stratified seeds (table II). Further, seeds stratified and incubated in light germinated to significantly higher percentages than those stratified in darkness and incubated in light (light-dark treatment,  $F_3 = 183.89$ ,  $P < 0.0001$ ; temperature regime,  $F_2 = 10.78$ ,  $P < 0.0001$ ; treatment  $\times$  temperature effect,  $F_6 = 7.96$ ,  $P < 0.0001$ ).



**Figure 1.** Germination percentages (mean,  $\pm 1$  SE if  $\geq 5$  %) of *Drosera anglica* seeds incubated in light at 15/6 (a), 20/10 (b) and 25/15 °C (c) for 2 (dark) and 4 (open) weeks following 0 to 18 weeks of stratification in light at 5/1 °C. Seeds were collected in 1999. ANOVA and PLSDs are based on germination after 4 weeks of incubation at test temperature regimes. Germination means after a given period of stratification indicated by the same lower case letter are not significantly different from each other, and those for a given temperature followed by the same upper case letter are not significantly different from each other.

### 3.4. Germination phenology

No seedlings emerged during the autumn or spring after sowing. In the succeeding summer, however, seven (1.2 %) seedlings were recorded. The first seedling was recorded on 24 June 1999 and the last on 12 August, i.e.  $> 9$  months after sowing. By 24 June, daily minimum temperatures exceeded 9 °C, and most maximum daily temperatures were  $> 20$  °C. Mean daily maximum and minimum temperatures from 20 June to 10 August were 22 and 14 °C, respectively. Average temperature recorded from 20 June to 10 August was 17 °C, while daily averages were between 13 and 22 °C.

## 5. DISCUSSION

Although 80 and 95 % of the *D. anglica* seeds collected in 1997 in Östergötland and in Gästrikland, Sweden, respectively, were viable (based on germination percentages from subsequent studies; see section 3.1), maximum germination of stratified seeds was only 13 %. There are various possible reasons why

**Table II.** Effect of 18 weeks of stratification at 5/1 °C in light and in darkness on germination percentages (mean  $\pm$  SE) of *Drosera anglica* seeds incubated in both light and in darkness for 4 weeks at three alternating temperature regimes<sup>a</sup>. Seeds were collected in 1999. ANOVA and PLSDs were calculated only for germination data after 4 weeks of incubation.

Stratification in	Incubation time (week)	Test temperature regimes ( °C)		
		15/6	20/10	25/15
Incubation in light				
Light	2	23 ± 5	81 ± 2	100
Light	4	87 ± 2 <sup>cA</sup>	95 ± 2 <sup>cAB</sup>	100 <sup>cB</sup>
Dark	2	0	1 ± 1	72 ± 8
Dark	4	6 ± 1 <sup>bA</sup>	82 ± 1 <sup>bB</sup>	91 ± 3 <sup>bB</sup>
Incubation in darkness				
Light	4	0 <sup>aA</sup>	0 <sup>aA</sup>	0 <sup>aA</sup>
Dark	4	0 <sup>aA</sup>	0 <sup>aA</sup>	0 <sup>aA</sup>

<sup>a</sup> Numbers in a column followed by the same lower case letter are not significantly different from each other, and those in a row followed by the same upper case letter are not significantly different from each other.

high germination percentages were not obtained. (1) The 2-week incubation period was not long enough to allow seeds to germinate. (2) Light was required during both the stratification and incubation periods to promote germination. (3) A 12-week period of stratification was not long enough to break dormancy. (4) The stratification temperature was too low for dormancy break to occur.

Seeds collected in 1999 and given 4 weeks of stratification in light germinated to 85 % during 2 weeks of incubation in light at 25/15 °C (figure 1). Also, 1999 seeds stratified in darkness for 18 weeks germinated to 72 % after 2 weeks of incubation in light at 25/15 °C (table II). Thus, of the four explanations for low germination percentages of the 1997 seeds, the 12-week period of stratification and the 2-week period of incubation should have been long enough, and light was not generally needed during stratification. Stratification treatments of 1998 and 1999 seeds were not conducted at a constant 1 °C, as was the case for 1997 seeds. A light tube (controlled by a time clock) placed inside a refrigerator increased the temperature from 1 to 5 °C during the period of illumination. Consequently, we used a 12/12 h daily temperature regime of 5/1 °C for stratification treatments. The effective temperature range for cold stratification of seeds is 0–10 °C [11, 30], with 5 °C being optimal for seeds of many species that require a moist low-temperature

treatment for dormancy break [30]. Thus, a daily temperature regime of 5 and 1 °C was well within the range of temperatures known to be suitable for cold stratification. As evidenced by 100 % germination in some of the tests (*tables I, II, figure 1*), the 5/1 °C regime was favorable for dormancy break in seeds of *D. anglica*. It appears that a constant temperature of 1 °C may have been too low for dormancy break of the 1997 seeds of *D. anglica*, or that dormancy break may require an alternating temperature regime rather than a constant temperature (e.g. [15]). The high germination percentage (ca. 90) that Crowder et al. [12] obtained after seeds of *D. anglica* had been stratified for 8 weeks (presumably in darkness) at a constant temperature of 10 °C suggests that the daily high temperature of 5 °C used in our stratification studies rather than the daily alternating temperature regime of 5 and 1 °C per se may have promoted dormancy break in the 1998 and 1999 seeds.

As mentioned previously, seeds of *D. anglica* were collected from the same site in Östergötland in 1997, 1998 and 1999. None of the freshly-collected 1997 and 1998 seeds germinated after 4 weeks of incubation in light at 15/5(6), 20/10 or 25/15 °C; however, 0, 3 and 5 % of the fresh 1999 seeds germinated at 15/6, 20/10 and 25/15 °C, respectively (*figure 1*). Thus, while none of the freshly-collected 1997 or 1998 seeds germinated at any condition at which they were tested, some of the 1999 seeds germinated in light at 20/10 and 25/15 °C; they were conditionally dormant. Another indication that the 1999 seeds were less dormant than the 1998 seeds is that a shorter period of stratification was required to obtain high germination percentages in the 1999 than in the 1998 seeds. Whereas the 1998 seeds germinated to only 22 % in light at 15/6 °C after 18 weeks of stratification in light (*table I*), the 1999 seeds germinated to 87 % (*figure 1*).

Year-to-year variation in germination of seeds produced at the same site has been attributed to differences in environmental conditions during the time seeds were maturing on the mother plant [5, 8]. Data recorded by the Swedish Meteorological and Hydrological Institute in Norrköping (58°58' N, 16°15' E), about 10 km south of the Östergötland *D. anglica* collection site reveal that mean daily maximum and minimum temperatures were 18.6 and 10.5 °C, respectively, for August 1998 and 21.5 and 10.3 °C, respectively, for August 1999 [31, 32]. Further, the average temperature in August 1998 and 1999 was 14.3 and 16.0 °C, respectively, and the average August temperature for 1961–1990 in Norrköping was 15.7 °C [31, 32]. Since seeds of *D. anglica* were collected in early

September, temperature data for August provide information on the conditions under which the seeds developed. Thus, the 1998 *D. anglica* seeds, which were more dormant than the 1999 seeds, matured at lower temperatures than the 1999 seeds. The ecological implication of these results is that with the same amount of cold stratification (*table I, figure 1*) seeds produced in warm summers gain the ability to germinate to higher percentages at 15/6 °C than those produced in cool summers. Thus, seeds produced in warm summers are more likely to germinate the following May when daily temperature regimes are about 15/6 °C, while germination of most seeds produced in cool summers would be delayed until June. Seeds used in the germination phenology study were produced in 1998 (cool summer), and their period of germination was from 24 June to 12 August 1999. Seeds of *Arenaria patula* Michx. var. *robusta* (Steierm.) Maguire that matured at relatively low temperatures (mean daily maximum and minimum temperatures 30 d prior to seed maturation were 26.4 and 10.4 °C, respectively) were also more dormant than those matured under relatively high temperatures (28.9 and 12.1 °C, respectively) [5].

The 1997 seeds were tested 3 d after collection, and the 1998 and 1999 seeds were tested 18 and 17 d, respectively, after collection. Thus, some afterripening (dormancy break) could have occurred in the 1998 and 1999 seeds prior to the time germination studies were initiated. However, since 1998 and 1999 seeds were stored at room temperatures for about the same period of time, the higher germination in the initial germination test of 1999 than in that of the 1998 seeds can not be attributed to length of the afterripening period prior to the time germination studies were started.

The 1998 and 1999 seeds tested in light at the alternating temperature regimes after various periods of stratification exhibited a decrease in the minimum temperature at which seeds would germinate with an increase in the stratification period (*table I, figure 1*). This kind of change in the temperature requirements for germination of seeds as they come out of dormancy was described by Vegis [33, 34], and Baskin et al. [4] called it a Type 2 response pattern. A Type 2 pattern has been found in many summer annuals and perennials in various plant families, including the Amaranthaceae, Asclepiadaceae, Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, Euphorbiaceae, Lamiaceae, Poaceae, Polygonaceae, Portulacaceae, Rosaceae, Scrophulariaceae and Solanaceae [1]. The presence of a Type 2 pattern in *D. anglica* seeds is the first report

of this response pattern in Droseraceae. Seeds of most species known to have a Type 2 response pattern are from the northern temperate region and require cold stratification for dormancy break; nevertheless, those of a few species in this region have a Type 2 response and come out of dormancy during summer. Since *Drosera* ranges from temperate to tropical regions of the world, it would be interesting to know if Type 2 is found in seeds of *Drosera* from throughout its range or only in *Drosera* species from temperate regions, where winter temperatures are suitable for cold stratification.

Dormancy break in seeds of *D. anglica* occurs during winter when environmental conditions in the habitat are not favorable for seedling establishment. However, a lowering of the minimum temperature for germination during cold stratification means germination can begin when temperatures are quite low in spring. Consequently, seedlings from spring-germinating seeds would have the maximum period of time for growth before temperatures drop below freezing in autumn. None of the *D. anglica* seeds germinated during the 18-week period in which they were being stratified in light at 5/1 °C, and germination of seeds stratified in light and incubated in light at 15/6 °C was slow (figure 1). Seeds stratified in light for 18 weeks germinated to 23 and 87 % after 2 and 4 weeks, respectively, in light at 15/6 °C. Thus, although seeds eventually may be able to germinate at simulated May field temperatures, temperatures in the field could increase above this level before seeds have enough time to germinate. In the germination phenology study, mean daily maximum and minimum temperatures for April 1999 were 10.8 and 4.5 °C, respectively; for May, 15.1 and 5.7 °C; and for June, 20.3 and 11.7 °C. Thus, little or no germination could be expected to occur until late May or June. In fact, the first seedling was not recorded until 24 June, by which time daily maximum and minimum temperatures were about 20 and 9 °C, respectively.

Dry seeds of *D. angelica* are ca. 1.6 mm in length and easily fit into Martin's [23] category of dwarf seeds, which are 0.3 to 2.0 mm in length. Since many dwarf seeds require light for germination (e.g. [2, 9]), it is not surprising that those of *D. anglica* also have this requirement. However, seeds of *D. anglica* not only required light for germination, but light had to be given after dormancy break had occurred (table II). That is, exposure to light during the cold stratification period did not promote germination in darkness at 15/6, 20/10 or 25/15 °C. In contrast, the light requirement for germination in some species with seeds greater than 2 mm in length can be fulfilled during

cold stratification (e.g. [3, 6]). Seeds of *D. anglica* stratified in darkness and incubated in light germinated at a slower rate and to a significantly lower percentage than those stratified in light and incubated in light (table II). The light requirement for germination may explain why so few seeds germinated in the phenology study. Frost-heaving of the soil in the pots may have resulted in many of the seeds becoming covered by soil particles; consequently, darkness would have prevented them from germinating. It seems reasonable that the dwarf, light-requiring seeds of *D. anglica* would form a soil seed bank, but to our knowledge this has not been demonstrated. However, persistent soil seed banks have been reported for *D. intermedia* [20] and *D. rotundifolia* [24, 28].

*Drosera anglica* is a perennial that reproduces mostly by seeds, but vegetative reproduction by axillary and leaf buds has been observed [12]. Sexual reproduction requires that seed germination be followed by successful seedling establishment and eventual seed production by plants. Seeds of *D. anglica* are dormant at maturity and require cold stratification for dormancy break. Length of the stratification period required for a high percentage of the seeds to germinate depends on (1) whether seeds are exposed to light during stratification and during the subsequent incubation period, and (2) the temperature during incubation (tables I, II, figure 1). Also, the year in which seeds mature may influence the amount of stratification needed to promote germination, especially at early spring habitat temperatures.

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